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REVIEW

Processing of Contrast Signals in the Insect Ocellar System

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INTRODUCTION

Most visual systems are designed to analyze space, and each array of their photoreceptors encodes light intensity at its narrow receptive field directed at different parts of the surrounding environment. The intensity signals are then converted into temporal and spatial contrast signals, i.e., the ratio of changes in light intensity in time and space, as a necessary pre-processing for detection of visual images. Indeed, all biologically significant visual information, such as movement, shape, and color of objects can be extracted from temporal and spatial contrasts but not directly from absolute light intensities. Although neural mechanisms for detecting spatial contrast are well examined, as reviewed by Laughlin [41], neural mechanisms for detecting temporal contrast are not well understood. This is mainly because the mechanisms for detecting temporal contrast signals are incorporated into complicated neural mechanisms for detecting more specific visual features such as spatial and color contrasts and movement, thus, it is almost impossible to separate neural circuits for detecting temporal contrast signals from those subserving advanced visual functions.

Insect ocelli are simple photoreceptive organs incapable of detecting shape, motion or color of small objects; they detect only intensity changes averaged over their large visual field. The ocelli, therefore, provide excellent material for studying neural mechanisms underlying the processing of temporal contrast signals. In this review I will summarize our present knowledge of the mechanisms underlying the processing of contrast signals in insect ocellar systems. This will include a discussion of spatial, temporal, and spectral properties of insect ocellar systems with special reference to their behavioral roles, as well as a review of neural organization of the insect ocellar system. I will examine the mechanisms to detect and process temporal contrast signals and summarize some neural principles underlying information processing in insect ocellar systems. I will then show that simple modifications and duplications of neural circuits for detecting temporal contrast signals are sufficient to explain neural circuits for detecting more elaborate visual features, such as the direction of motion. Finally, I will discuss possible evolutionary pathways by which advanced neural networks subserving advanced visual functions have emerged from simpler neural networks subserving simpler visual functions.

FUNCTIONAL PROPERTIES OF INSECT OCELLI

Most adult insects possess two or three ocelli in addition to a pair of compound eyes. Three ocelli is the usual number but some insects like cockroaches and moths have two ocelli. The compound eyes are sophisticated visual organs responsible for functions that require good spatial resolution, such as the perception of movement, fixation of objects and pattern recognition. In contrast, the ocelli are simple photoreceptive systems with very poor spatial resolution [21]. Why then do insects need simple photoreceptors, i.e., ocelli, even though they are equipped with sophisticated compound eyes? Although this question has not been fully resolved, some answers have emerged recently from extensive anatomical, physiological and behavioral studies [51].

Insect ocelli possess high-aperture dioptrics which exhibit wide visual fields [9, 21, 82]. Measurements of the focal length of the ocellar lens show that the image plane lies well behind the retinal receptory layer. Due to underfocussing, an object entering the ocellar visual field results in a change in the light intensity impinging on the photoreceptor layers rather than the formation of an image. The output of a large number of photoreceptor cells converges upon a small number of large second-order neurons, called L-neurons [21]. Such a system is best suited for the detection of small changes in light intensity integrated over its wide visual field [111]. Thus, the ocelli are specialized for the effective capture of photons, at the cost of spatial resolution.

The spectral properties of ocellar L-neurons are characterized by broad spectral tuning with sensitivity to both ultraviolet (UV) and visible light. Ocellar spectral sensitivity curves have a marked UV peak with an additional peak in either the blue (in flies [31, 34]) or green (in dragonflies [6], locusts [111], moths [14, 69], and honeybees [19]). The combined UV-blue or UV-green sensitivity in the ocelli appears to be an adaptation for increased sensitivity.

Although the ocelli of most insects have sensitivity to both UV and visible light, a few insects living in extreme light

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environments have ocelli with only UV or green sensitivity. Mote and Wehner [59] found that the ocelli of desert ants, which live under bright and UV-rich sunlight, have only a UV peak and are not sensitive at wavelengths longer than 445 nm. The ocelli of some nocturnal insects which rarely encounter UV-rich sunlight such as field crickets, *Gryllus firmus* [40] and cockroaches, *Periplaneta americana* [19] have only single receptor systems maximally sensitive to green and not sensitive to UV. These examples nicely fit the theory that visual pigments have evolved in accordance with environmental light conditions.

Measurement of the absolute sensitivity of large second-order ocellar neurons, called L-neurons, of the locust suggests that the sensitivity of ocelli is at least several times as high as that in compound eyes. Wilson [111] concluded that L-neurons of locust ocelli are 5 times more sensitive to a point source than lamina monopolar cells, a major class of second-order neurons of compound eyes. Wilson [111] also concluded that L-neurons of locusts are 5000 times more sensitive to extended sources than the lamina monopolar cells, although pooling of signals from monopolar cells could improve the sensitivity of higher visual neurons.

What are the advantages of having high sensitivity? Light intensity is defined as the average number of photons per unit time, and the fewer the photons, the larger is the uncertainty about the true average. The absolute sensitivity, i.e., the effectiveness in catching a photon and converting it to a voltage signal, is an essential limiting factor for visual systems. In any arbitrary visual system, increased absolute sensitivity can be used to see at lower intensities, to see faster events, or to detect objects of less contrast.

There is evidence to show that ocelli contribute to low light intensity perception. Schricker [81], for example, examined phototactic runs of honeybees where bees could choose between two lights. He noted that a significantly greater number of them chose the brighter light. Below 1 Lux, only a two-fold difference of intensity was needed for this to occur. Bees with one ocellus blinded needed a four-fold difference, bees with two ocelli blinded needed a six-fold difference and bees with all their ocelli blinded needed an eight-fold difference before a significantly greater number of the bees chose the brighter of the two lights.

Initiation and cessation of diurnal activities of insects often depend on light intensity levels [12, 81]. Under natural environmental conditions where the light-dark cycle consists of dawn and dusk ramps, it would be advantageous for insects to be sensitive to minute changes in illumination. There is evidence to show that signals from ocelli are utilized to determine the threshold light intensity for diurnal activities in bees [23, 81], moths [15, 92] and crickets [74]. In the bee, the first and last of its daily flights is dependent upon the intensity level [81]. If the ocelli are occluded, foraging bees behave normally in most respects [81]. Occlusion of the ocelli, however, does interfere with the timing of the first and last foraging flights. Bees with one, two or three ocelli occluded start to collect food later in the morning and cease collecting earlier in the evening than normal workers. The light intensity required for the first and last collecting flight is increased by a factor of two if one ocellus is covered, 3.3 if two ocelli are covered and 4.5 if all the ocelli are covered. Further evidence of an ocellar contribution to low light intensity perception is reviewed by Mizunami [51].

Another notable advantage of ocelli over compound eyes is the higher speed of signal transmission. In bees, the latency of ocellar and compound eye pathways were measured in descending multimodal neurons which receive inputs from both the compound eyes and ocelli [25]. The descending neurons received ocellar input before the arrival of the delayed compound eye input. The latency of ocellar pathways was 9 msec, while that of the compound eye pathway was 25–35 msec.

For fast-flying insects, the ability to perform rapid visual steering is essential for survival. There is evidence to show that insect ocelli contribute to rapid visual steering in flight. Taylor [101] measured the delay of the head motion response of a tethered locust after the motion of an artificial horizon. Both the ocelli and compound eyes were involved in this response. The delay was 45.4 ± 4 msec when all eyes were intact. The delay was almost unchanged when the compound eyes were ablated (47.4 ± 12 msec) but significantly increased when the ocelli were cauterized (103.4 ± 7 msec), thereby demonstrating that the high speed of signal transmission by the ocelli contributes to shortening the latency of the locust's response to motion of horizon.

The perfect suitability of insect ocelli for detecting movement of the horizon, i.e., the contrast between the earth and sky, and for stability control in flight have been discussed in detail [29, 111]. Wilson [111] argued that locust ocelli have a large receptive field directed horizontally, providing the animal with heavily blurred neural images of the skyline, where unwanted information about structural details are eliminated. Ocellar sensitivity to UV facilitates horizon detection since the contrast between bright sky and dark ground is highest in UV. The high speed of signal detection and transmission in the ocellar system is ideal for rapid course control. Pitch and roll deviation of the flight course are independently detectable by the combination of signals from three ocelli. A roll (turning around the long axis of the body) will cause no change in signal from the median ocellus but will tend to cause a decrease of illumination in one lateral ocellus and an increase in the other lateral ocellus. Detection of pitch can be achieved through measurement of the output of the median ocellus. This hypothesis was confirmed by behavioral studies in dragonflies [93, 94] and locusts [20, 100, 101]. The neural mechanisms underlying the ocellar contribution to the flight steering are well established in locusts [24, 73, 75, 85].

In conclusion, although the ocelli can detect only intensity changes averaged over its large receptive field, they are superior to the co-existing compound eyes in sensitivity and speed. Thus, the ocelli play a major role in insects where functions such as stability control in flight and low light intensity perception require for high speed or high sensitivity. Insects have successfully extended the range of visual stimuli to which they can respond by having two fundamentally different visual systems, i.e., compound eyes and ocelli, the former designed to attain a high spatial resolution and the latter to attain a fast signal transmission and a high absolute sensitivity. The specific functional design of insect ocelli makes them a suitable model system for examining the neural basis of the processing of temporal contrast signals.

NEURAL ORGANIZATION OF THE COCKROACH OCELLAR SYSTEM

The neural circuits of the insect ocellar system have been studied in a number of species including locusts [22, 44, 90] and bees [25, 68]. Here I will briefly discuss the neural organization of the cockroach ocellar system, as a representative example. Comparative aspects of the neural circuits of insect ocellar systems have been discussed (Mizunami, submitted). Cockroaches have two ocelli, each of which contains about 10,000 photoreceptor cells [108], which converge synaptically upon four large second-order neurons in the ocellar plexus [10, 55, 104]. The large second-order neurons, called L-neurons, exit the ocellus and project into the ocellar tract neuropil of the protocerebrum, through the ocellar nerve (Fig. 1) [52, 55]. Electron microscopic studies show that the ocellar nerve and the ocellar tract are a continuous neuropil area where second-order neurons make synaptic interactions with third-order and efferent neurons [102; 104]. The morphology and physiology of neurons involved in the cockroach ocellar system have been successfully identified by combining extracellular and intracellular staining techniques [52, 55, 63, 64, 65, 105]. Recently, the number and gross morphologies of interneurons in the ocellar tract neuropils were estimated by injecting cobalt ions into the ocellar tract neuropil via microelectrodes. Cobalt ions were taken up and transported by neurons in the ocellar tract; thus, the morphologies of these neurons could be revealed by subsequent histological treatment. By comparing the morphologies of neurons in more than 50 cobalt-filled preparations, it was concluded that each ocellar tract neuropil contains at least 25 interneurons. Twenty-two out of 25 neurons have been characterized anatomically and physiologically by intracellular recordings and stainings [52, 55, 64, 65; Mizunami, submitted], which are: (1) four large second-order neurons projecting into the ocellar tract [55], (2) 16 third-order neurons [52, 55; Mizunami, submitted] which receive monosynaptic inputs from second-order neurons in the ocellar nerve and the ocellar tract [54, 102, 104] and project into various neuropil areas of the brain, (3) two possible efferent neurons modulating the activity of large second-order neurons [64]. Morphology of some of the third-order neurons are shown in Fig. 2. The remaining three neurons still to be characterized. The projection areas of the third-order ocellar neurons include: (1) visual, olfactory and mechanosensory centers, (2) the mushroom body (a higher associative center) [58], (3) premotor centers, including the posterior slope, from which descending brain neurons originate [97, 98] and (4) the thoracic motor systems. The abundance of target neuropil areas in the cockroach ocellar system suggests a multiplicity of ocellar functions: (1) to modulate the activity of visual, olfactory and mechanosensory systems, (2) to influence the activity of higher associative centers, (3) to modulate the activity of descending brain neurons and (4) to produce direct behavioral actions. The projection areas of ocellar neurons of the cockroach are more or less similar to those reported for other insects including locusts [22], bees [68], and crickets [39]. In conclusion, the neural organization of the cockroach ocellar system is summarized as follows: (1) the large number of photoreceptors converge onto only a very small number (four) of second-order neurons in the ocellar plexus and (2) in the ocellar tract neuropil, second-order neurons synapse onto a large number of third-order neurons which project into a number of target neuropils.

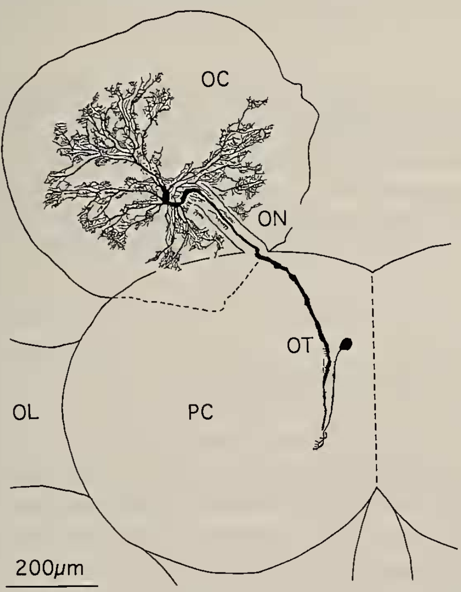

Fig. 1. Morphology of an large second-order neuron (L-neuron) of the cockroach ocellus. The L-neuron extends their dendritic branches into the ocellar plexus, and its axon projects into the ocellar tract neuropil of the protocerebrum, through the ocellar nerve. OC, ocellus; ON, ocellar nerve; PC, protocerebrum; OT, ocellar tract neuropil; OL, optic lobe. Viewed posterodorsally. Modified from Mizunami *et al.* [56].

LINEAR PERIPHERAL MECHANISMS FOR THE DETECTION OF CONTRAST SIGNALS

An effective approach for understanding information processing in the ocellar system is to analyze the dynamics and sensitivity of the responses of its interneurons to changes in light intensity around a mean level, because this system is characterized by a high sensitivity for detecting changes in intensity and high speed for transmitting them to various target neuropils including thoracic motor centers. Analysis

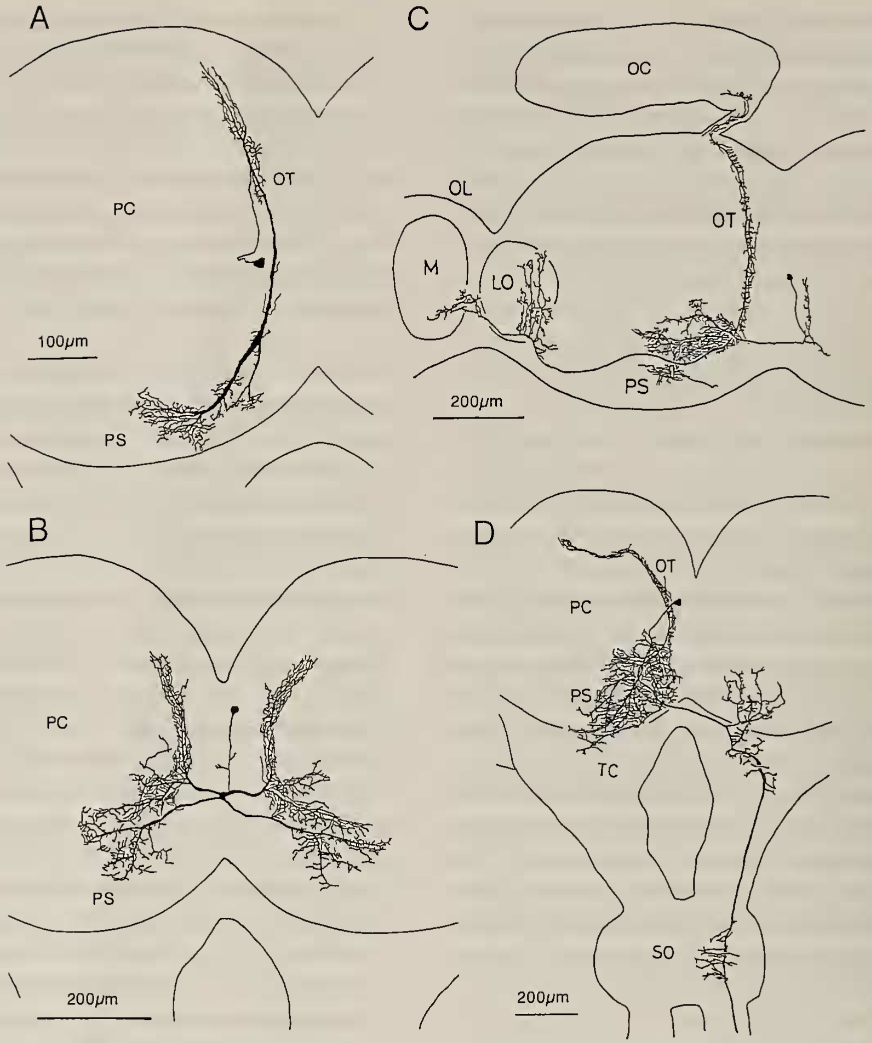

Fig. 2. Examples of third-order ocellar neurons of the cockroach ocellar system. Viewed postero-dorsally. (A) A PS-I neuron which arborizes in an ocellar tract and projects into the ipsilateral posterior slope. (B). A PS-III neuron which arborizes in bilateral ocellar tracts and projects into bilateral posterior slopes. (C) A OL-I neuron which projects into the lobula and medulla of the optic lobe. (D) A D-I neuron which arborizes in the ocellar tract, posterior slope and tritocerebrum. Its axon descends contralaterally toward the thoracic ganglia. There is evidence to show that these neurons receive monosynaptic inputs from L-neurons [54]. OC, ocellus; PC, protocerebrum; OT, ocellar tract neuropil; PS, posterior slope; OL, optic lobe; M, medulla; LO, lobula; TC, tritocerebrum; SO, suboesophageal ganglion. Modified from Mizunami and Tateda [52].

of intracellularly-recorded responses of ocellar neurons to changes in light intensity was pioneered by Chappell and Dowing [7] who studied the responses of photoreceptors and the second-order neurons of dragonfly ocelli, and discussed signal processing at synapses between them, which I refer to as first synapses. Subsequently, Mizunami and his colleagues [49, 53, 54, 56] have analyzed response properties of second- and third-order neurons of cockroach ocelli and examined information processing at synapses between second and third-order ocellar neurons, which I refer to as second synapses, by using white-noise and sinusoidally modulated light. This section deals with information processing by photoreceptors and second-order neurons. Further processing of contrast signals by higher-order neurons will be discussed in the next section.

Signal processing at first synapses

Insect ocelli contain a large number of photoreceptors which make synapses with a small number of large second-order neurons, called L-neurons. Both the photoreceptors and L-neurons generate graded, slow potential responses to light stimuli. Photoreceptors exhibit a depolarizing response to a step of light given in the dark, whereas L-neurons exhibit a hyperpolarizing response (Fig. 3A, B) [7, 35, 70, 88]. The hyperpolarizing response of L-neurons is due to an increase in membrane permeability to ions whose equilibrium potential is negative to the membrane potential in the dark [111].

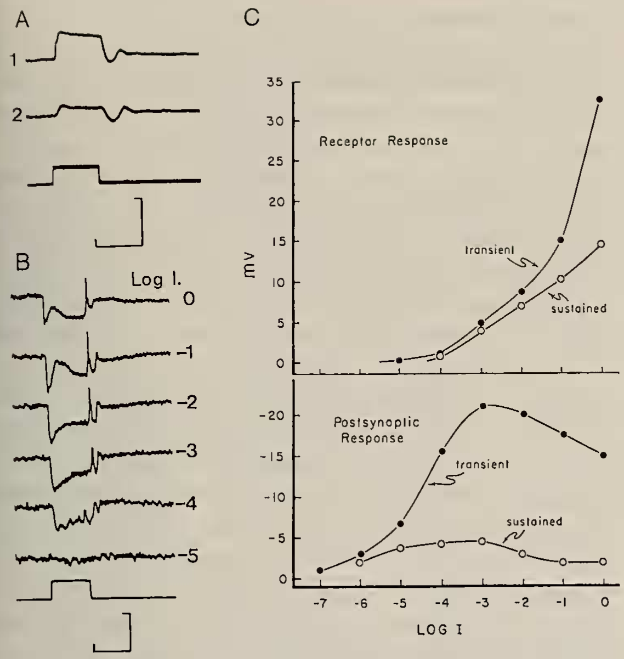

FIG. 3. Responses of a photoreceptor and a large second-order neuron of the median ocellus of the dragonfly, *Aeschna*. Intracellularly recorded responses of a photoreceptor (A) and a large second-order cell (B) to illumination of the median ocellus with pulses of white light at different intensities Log I, $\log_{10}$ relative intensity of illumination. Scales: 200 ms; 20 mV. (C) Intensity-response relationships for receptor and postsynaptic units. The amplitude of the peak of the transient wave and the sustained component of the receptor response and the postsynaptic response are plotted as a function of intensity. The sustained component of the receptor response was measured 3 sec after the start of illumination. A and B are from Patterson and Chappell [70]; C is from Chappell and Dowling [7].

Chappell and Dowling [7] have compared responses of photoreceptors and L-neurons of dragonfly ocelli to a step of light given in the dark, and have noted two important differences between the responses of photoreceptors and L-neurons. First, the sensitivity of L-neurons is larger than that of photoreceptors by 1–2 log units (Fig. 3A, B). This is explained by a high ratio of convergence of photoreceptors onto L-neurons [11]. Second, the waveform of the response of L-neurons is much more transient (Fig. 3A, B), and the sustained component of the response of L-neurons is much less prominent (Fig. 3C) than that of photoreceptors.

The functional significance of the enhancement of transience was clarified by further examinating the responses of photoreceptors and second-order neurons to changes in light intensity around a mean level [7, 56]. The photic inputs that visual systems receive naturally is a modulation of light intensity around a mean illuminance. The mean illuminance changes slowly but covers a large range in the course of one day. The depth of fluctuation around the mean is moderate and remains roughly constant. The photoreceptor response to changes in intensity consists of two components, a steady mean potential and a time-varying component, which signal mean illuminance levels and intensity changes, respectively. The steady response component of L-neurons, however, is highly compressed (in dragonflies [7, 56, 88]) or completely eliminated (in bees [3]), indicating that L-neurons signal relative intensity changes rather than absolute light intensity level. It is concluded that, at the first synapses, the photoreceptor responses signaling absolute intensity level is high-pass filtered to produce a postsynaptic response signaling about relative intensity change. The enhancement of the response to intensity changes by temporal highpass filtering have been noted at first synapses of most visual systems studied so far, including barnacle ocelli [28, 95, 99], insect compound eyes [42, 84, 109], *Limulus* lateral eyes [72] and vertebrate retinas [4, 60, 62, 110]. This apparent common principle among visual systems reflects the fact that visual systems are designed to detect the contrast between objects and background in the presence of background illumination, rather than the light intensity itself.

Dowling and Chappell [11] performed an electron microscopic study of the dragonfly ocellar plexus and found that L-neurons make observed feedback synapses onto photoreceptors. They [11] proposed that these feedback synapses play major roles in the temporal highpass filtering. Klingman and Chappell [35] have studied the effects of various drugs on the response of L-neurons in dragonflies and suggested that the receptor synapses are inhibitory (sign-inverting) and curare-sensitive, whereas there are excitatory (sign-conserving) GABAergic feedback synapses from L-neurons which facilitate photoreceptor transmitter release. Stone and Chappell [96] have suggested that hyperpolarizing oscillation at the off-set of illumination in dragonfly photoreceptors reflects GABAergic feedback synapses onto photoreceptor terminals. Subsequent studies, however, have failed to confirm the feedback hypothesis for the enhancement of response transience. Simmons [87] made simultaneous intracellular recordings from a photoreceptor and an L-neuron of a dragonfly ocellar retina; no response was evoked in the photoreceptors when depolarizing or hyperpolarizing currents were injected into L-neurons, although L-neurons produced responses when current was injected into photoreceptors. In addition, no immunoreactivity to GABA was observed from L-neurons, at least in locusts [2] and bees [80]. Unfortunately, GABA-immunocytochemical studies have not been performed on dragonfly L-neurons. The response of bee L-neurons is very phasic [25], although no feedback synapses have been observed between L-neurons and receptors in the bee [103]. There should be a mechanism to enhance the transience other than the feedback from L-neurons, at least in the bee. Simmons [87] proposed that the intrinsic membrane properties of the photoreceptor terminals and L-neurons, and excitatory synapses made by small second-order neurons on L-neurons are included in the mechanisms to enhance the response transience of dragonfly L-neurons. Ammermüler and Weiler [85] discussed the possible contribution of GABAergic small second-order neurons in a feedback system of the locust. In summary, neural mechanisms underlying the enhancement of response transience at first synapses of insect ocelli still to be established.

Dynamics of slow potential responses of second-order neurons

The most extensive analysis of responses of ocellar L-neurons have been made in the cockroach by using white-noise modulated light with various mean illuminances (Fig. 4) [56]. The kernels, obtained by cross-correlating the white-noise input against the resulting response, provided a measure of incremental sensitivity as well as of response dynamics (Fig. 5). The first-order kernels, the product of first-order cross-correlation, represent the linear component of the cell's response, and second- and higher-order kernels, products of second- and higher-order cross-correlation, represent the nonlinear components of the response.

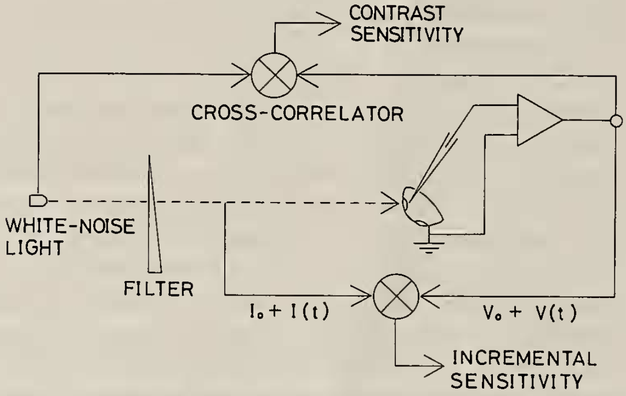

Fig. 4. Schematic drawing of experimental procedure to study incremental response of cockroach ocellar L-neurons. A series of ND filters were interposed between the light source and the preparation to attenuate both the mean illuminance and white-noise modulation by the same proportion, so that the "contrast" of the stimulus was kept unchanged. The light signal was monitored before it was attenuated by filters and a correlation was made between the unattenuated light signal and the cellular response. The correlation produces kernels on a contrast sensitivity scale. Kernels were converted to an incremental sensitivity scale by multiplying the kernel's amplitude by the attenuation factor. From Mizunami *et al.* [56].

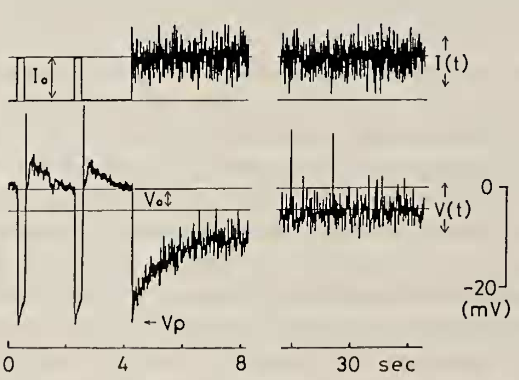

Fig. 5. Responses from a cockroach ocellar L-neuron evoked either by steps of light given in the dark or by white-noise-modulated light. The relationship between I_0 and V_p or V_0 is the cell's DC (static) sensitivity and the relationship between I(t) and V(t) is incremental sensitivity. Spike potentials are seen at the offset of step stimulation as well as during white-noise stimulation. From Mizunami *et al.* [56].

A brief step of light given in the dark produced step-like hyperpolarization in L-neurons. At the off-set of light stimulation, L-neurons generate solitary spikes. Here I will concentrate on the slow potential response of L-neurons; their spike response will be discussed in the next section. With continued white-noise stimulation, the membrane potential reaches a steady level within 30 sec (Fig. 5). At this dynamic steady state, the actual responses of L-neurons to white-noise stimulus can be predicted by a linear model (Fig. 6) with mean-square-errors of about 11%. This indicates that the response is practically linear, i.e., the magnitude of the response is proportional to the depth of modulation. The linear nature of the response to intensity changes has been reported from peripheral visual neurons in a variety of visual systems including the photoreceptors of the *Limulus* compound eye [18], vertebrate retina [5, 61] and insect compound eye [71], as well as the second-order neurons of vertebrate retina [8, 60, 107], the *Limulus* compound eye [38] and insect compound eye [17]. Linear coding of photic signals thus appear to be a general principle of peripheral visual systems.

In Fig. 7, first-order kernels which represent the linear

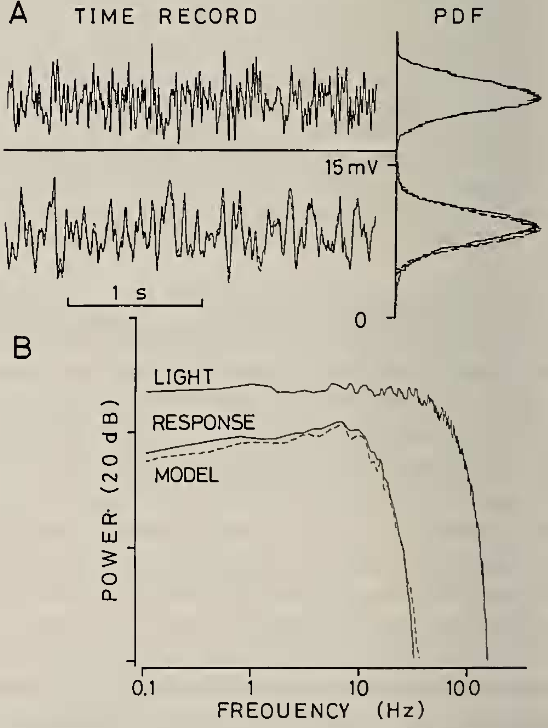

Fig. 6. Responses of a cockroach ocellar L-neuron to a white-noise modulated light. (A) Time records of part of a white-noise stimulus and the resulting response of a cockroach L-neuron (continuous line). Superimposed on the response trace is the linear model (broken line). Probability distribution function (PDF) for the light stimulus and the recorded response are also shown. The light PDF is also superimposed on the response PDF. (B) Power spectra of the light stimulus, response (continuous line), and linear model (broken line). The mean illuminance of the stimulus is 20 μW/cm^2. From Mizunami *et al.* [56].

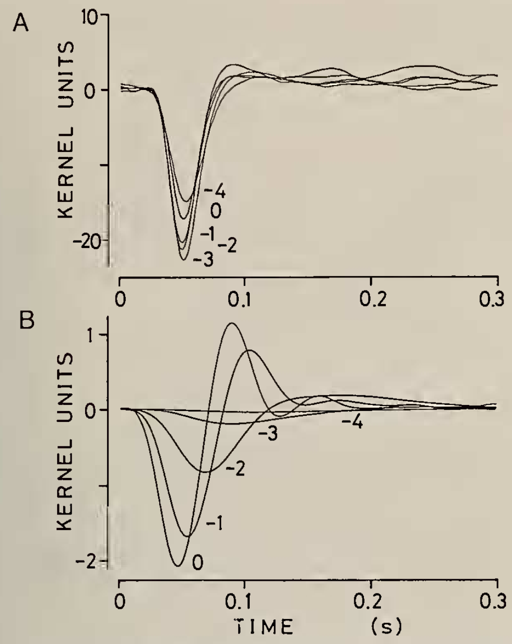

Fig. 7. Comparison of first-order kernels of second-order neurons of cockroach ocelli and vertebrate retinas. (A) First-order kernels from a cockroach ocellar L-neuron, plotted on a contrast sensitivity scale, obtained at five mean illuminance levels. The first-order kernels were calculated by cross-correlating the white-noise light stimuli with the recorded responses. Kernels are labeled 0 through −4 to indicate the log density of the filters interposed. Note that the amplitudes of the kernels did not differ by more than 30% and the peak response times were constant at 50 msec for all kernels, although the mean levels covered a range of 1 : 10,000. Stimuli dimmer than −4 log units did not produce any reliable results. (*B*) First-order kernels from a turtle retinal horizontal cell, plotted as in *A*. The peak response times, waveforms, and amplitudes differed at various levels of mean illuminance. Kernel units are in millivolts per microwatt per square centimeter per second. The larger incremental sensitivity for ocellar kernels was due to a dimmer mean illuminance ($20\mu W/cm^2$ at 0 log) of the white-noise stimulus than in the turtle experiment ($50\mu W/cm^2$ at 0 log). From Mizunami *et al.* [56].

component of the response obtained at four log ranges of mean luminance levels have been plotted on a contrast sensitivity scale. The waveforms are almost identical, with constant peak response times of about 50 msec, while the amplitudes differ only by 30%. The results show that the response is an exact Weber function, i.e., contrast sensitivity remains unchanged over at least a four log range of mean illuminance levels and that the response dynamics remains unchanged at the same range of mean illuminance levels. For comparison, an example of kernels from a horizontal cell of turtle retina obtained under comparable conditions is shown in Fig. 7, where the amplitude of kernels differs at different levels of mean illuminance, the peak response times shorten from 100 to 50 msec, and the waveforms become more biphasic (differentiating) with an increase in mean luminance. These studies show that (1) the cockroach L-neurons are ideal contrast detectors since their response amplitude is exactly proportional to the contrast of intensity change for at least 4 log ranges of mean illuminance levels and (2) signal processing in the cockroach ocellus differs from other visual systems, including *Limulus* lateral eyes [18], insect compound eyes [13, 71], vertebrate retinas [5, 60], and the human visual system [33], in that the system's dynamics change depending on the levels of mean illuminance. Frequency-response characteristics of L-neurons have also been studied using sinusoidally-modulated light [49, 54]. The response of L-neurons is bandpass with an optimal frequency of 1–3 Hz, a lower cut-off frequency (−3 dB) of 0.05–0.1 Hz and a higher cut-off frequency of 12–15 Hz, indicating that this neuron can respond to slowly occurring events.

Interestingly, there are marked differences in incremental responses of light-adapted L-neurons among different insects. Contrast sensitivity of bee L-neurons [3] is much lower than that of the cockroach [56], i.e., they can not respond to stimuli of small contrast. However, some L-neurons of the bee exhibit a higher cut-off frequency of about 30 Hz [3], and thus can respond to stimuli of much higher frequency than can cockroach L-neurons. These findings are consistent with the hypothesis proposed by Mizunami (in preparation) that the ocellar system of the bee is more concerned with speed than sensitivity, while that of the cockroach is more concerned with sensitivity than speed. In addition, the waveform of the response of bee L-neurons to sinusoidally-modulated light highly deviates from sinusoid [3], indicating that the response contains a high degree of nonlinearity. The bee L-neurons are not suited to faithfully monitoring the stimulus contrast, and are perhaps more related to the initiation of direct behavioral reactions. Furthermore, Simmons [89] has recently measured frequency response characteristics of locust L-neurons using sinusoidally modulated light, and has noted that the optimal frequency, where the contrast sensitivity is highest, changes from 2 Hz to 10 Hz with an increase in mean illuminance levels. Since such changes have not been observed in the responses of cockroach L-neurons [56], ocellar systems of locusts and cockroaches must adopt different strategies to adjust their response dynamics to environmental light intensity levels. Such differences may imply that there are fundamental differences between the behavioral roles of locust and cockroach ocelli, a possibility which should be examined further.

NONLINEAR CENTRAL MECHANISMS FOR THE PROCESSING OF CONTRAST SIGNALS

The signals about temporal contrast encoded in the graded responses of ocellar L-neurons are further processed to detect specific visual features. In the following section, I will first discuss signal conversion at the spike initiation process in L-neurons, and then discuss signal processing at synapses from second- to third-order neurons (second synapses) of cockroach ocellar system.

Dynamics of the spike initiation process in L-neurons

L-neurons of most insects respond to light stimuli with regenerative spikes, in addition to graded slow potentials (cockroaches [55, 57]; bees [45, 46]; locusts [88, 112]). The relationship between the slow potential and spikes of L-neurons have been analyzed in the cockroach using a sinusoidally modulated light with various mean illuminances [53]. L-neurons generated a solitary spike at the depolarizing phase of the modulation response (Fig. 8). The relationship between the peak-to-peak amplitude of the slow potential response and the rate of spike generation was sigmoidal, with a linear part covering the spike rate ranging from 10 to 90% (Fig. 9A). In Fig. 9B, the spike rate has been plotted against the amplitude of the slow potential response at five different frequencies. The results at a spike rate of between 10 to 90% are shown. The extrapolated regression lines for each frequency cross the vertical axis at almost the same point, suggesting that the nonlinear threshold is frequency independent. In contrast, the slope of the lines changes with frequency, which indicates that the spike initiation process contains dynamic linearity. Subsequent studies have shown that the spike threshold at optimal frequency (0.5–5 Hz) remains unchanged over a mean illuminance range of 3.6 log units, whereas the spike threshold at frequencies of <0.5 Hz was lower at a dimmer mean illuminance (Fig. 10A), where the L-neurons exhibited a larger voltage noise and their mean membrane potential levels were more positive (Fig. 10B). Steady or noise current injection during sinusoidal light stimulation showed that (1) the decrease in the spike threshold at a dimmer mean illuminance was due to an increase in the noise variance, i.e., the noise had a facilitatory effect on the spike initiation and (2) the change in the mean potential level had little effect on the spike threshold (Fig. 11). In summary, the spike response of L-neurons is repre-

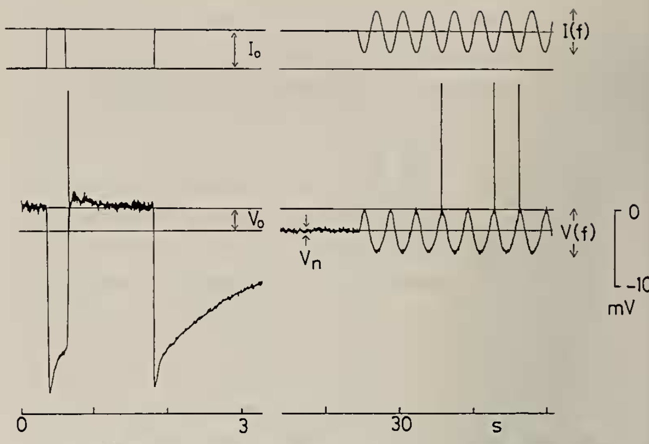

Fig. 8. Responses of a cockroach ocellar L-neuron evoked either by a step light stimulus given in the dark or by a sinusoidally modulated light stimulus. The L-neuron responded to the sinusoidal stimulation with a sinusoidal voltage modulation, $V(f)$, around a mean voltage, V_o. A spontaneous voltage fluctuation (voltage noise), V_n, was superimposed on the modulation response. Spikes were seen at the offset of step stimulation and at the peak of the voltage modulation. The mean illuminance of the stimulus, I_o, was $20\,\mu\text{W}\cdot\text{cm}^{-2}$; the modulation frequency, f, was 2 Hz; the depth of modulation of the stimulus, $I(f)$, was 60%. From Mizunami and Tateda [53].

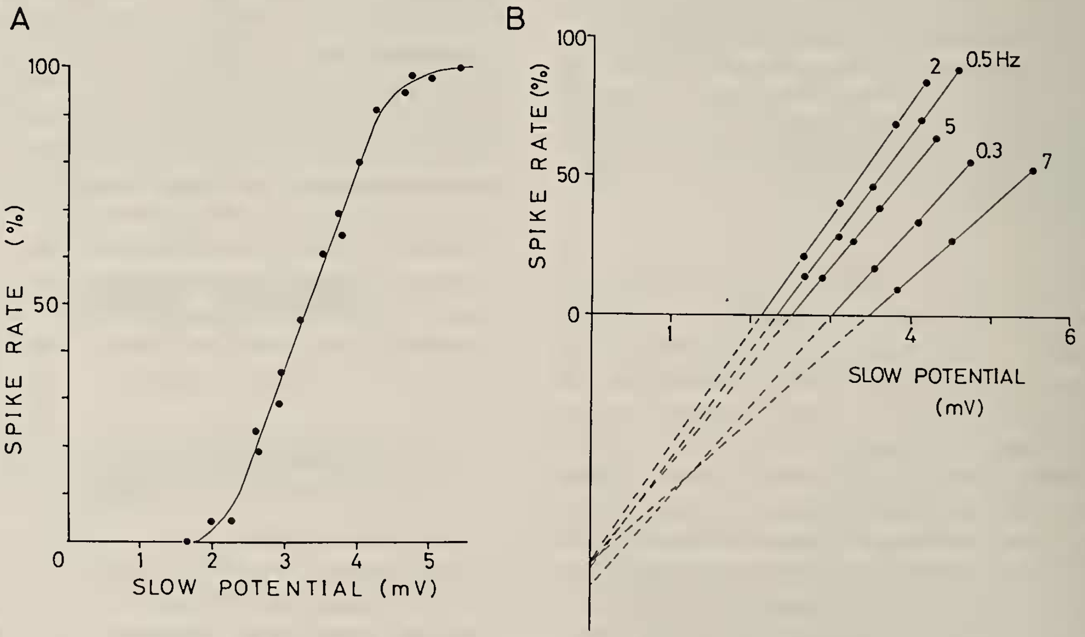

Fig. 9. Dynamics of the spike initiation process in a cockroach ocellar L-neuron. (A) The rate of spike generation plotted against the peak-to-peak amplitude of the slow potential response of a cockroach L-neuron, obtained at a frequency of 1 Hz. The form of the curve was sigmoidal, with the linear part covering the range of spike rate from ∼10–90%. (B) The spike rate plotted against the amplitude of the slow response of a cockroach L-neuron, obtained at five different frequencies. The extrapolated broken lines are the regression lines for each frequency. These lines cross the vertical axis at almost the same point. The stimulus had a mean illuminance of $2\,\mu\text{W}\cdot\text{m}^{-2}$. From Mizunami and Tateda [53].

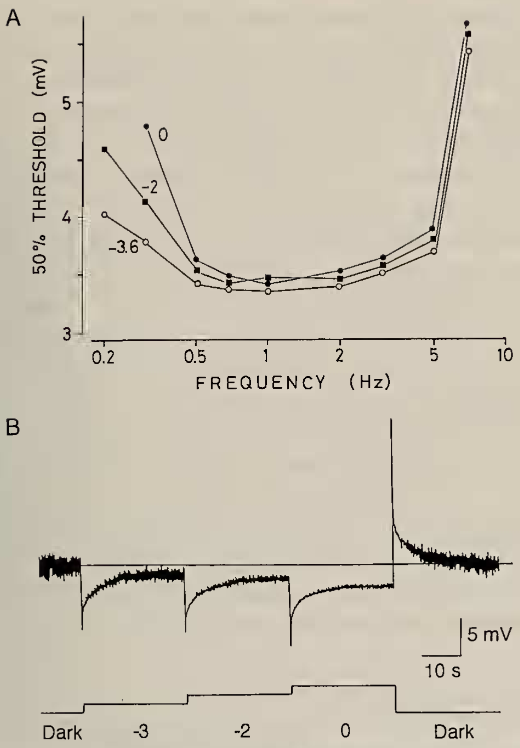

FIG. 10. Effects of mean illuminance changes on the dynamics of the spike initiation process in a cockroach L-neuron. (A) 50% threshold of spike response, defined as the peak-to-peak amplitude of the potential modulation at a spike rate of 50%, plotted against the modulation frequency. The plots are from the responses of a cockroach L-neuron to sinusoidal lights with a mean illuminance of 0.005 (−3.6 log), 0.2 (−2 log), and 20 μW·cm^{-2} (0 log). (B) Responses of a cockroach ocellar L-neuron to prolonged illuminations. The light intensities are indicated as $\log_{10}$ attenuation (0 log units=20 μW·cm^{-2}). From Mizunami and Tateda [53].

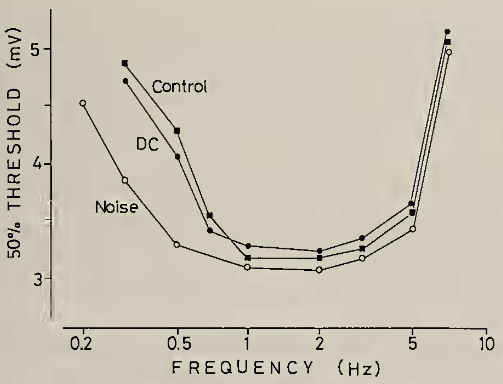

FIG. 11. Effects of noise current and steady current injection on the 50% threshold of a cockroach L-neuron. A noise current having a peak-to-peak amplitude of ~4 nA or a steady depolarizing current of 4 nA was injected during sinusoidal light stimulation. The light stimulus had a mean illuminance of 20 μW·cm^{-2}. The estimated potential change produced by the injection of a 4 nA current was ~3 mV (the estimated input resistance at that mean illuminance was ~0.8 MΩ). The 50% threshold at a low-frequency range decreased when the noise current was injected. The steady depolarizing current had little effect on the 50% threshold. From Mizunami and Tateda [53].

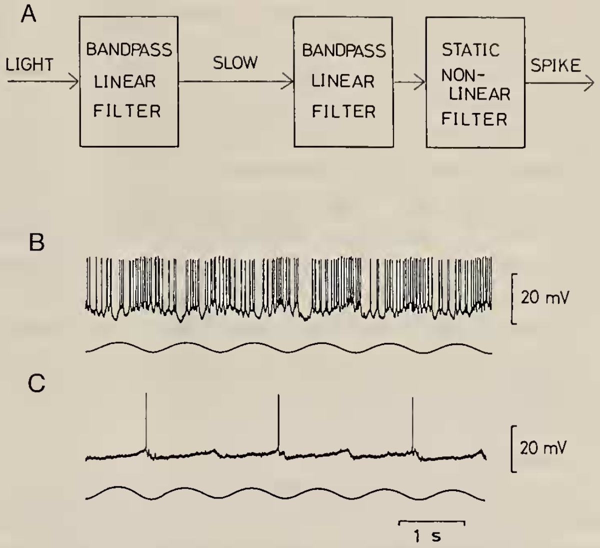

FIG. 12. (A) A model for the spike response of cockroach ocellar L-neurons. Light signals are passed through a bandpass linear filter, producing a slow potential response in L-neurons. The slow potential contains a noise which reflects that contained in the synaptic potential from photoreceptors. The slow potential is further passed through a linear/nonlinear cascade and produces a spike discharge. The linear filter is bandpass, and the nonlinear filter is a static threshold. (B, C) Typical responses of two types of third-order ocellar neurons of the cockroach to sinusoidal light stimulation. One type of third-order neuron, the OL-I neuron (type 1 neuron projecting into the optic lobe), showed sinusoidal modulation of spike frequency (B), whereas the other type, the D-I neuron (type 1 neuron descending to the thoracic ganglia), generated solitary spikes at the decremental phase of light modulation (C). The lower traces indicate the stimulus light, monitored by a photodiode. The stimulus had a modulation frequency of 1 Hz and a modulation depth of 50%. The mean illuminance was 2 μW·cm^{-2}. From Mizunami and Tateda [53].

sented by a simple cascade model (Fig. 12A). A light stimulus is passed through a bandpass linear filter and produces a slow potential response in L-neurons. The slow potential is passed through a cascade of a linear filter followed by a nonlinear filter and produces a spike discharge in L-neurons. The linear filter is bandpass containing both a differentiating and an integrative nature. The nonlinear filter is a static threshold with a sigmoidal (probablistic) input/output relationship. It is concluded that fundamental signal modifications occur during spike initiation in cockroach L-neurons, a finding which differs from the spike initiation process in other visual systems, including the *Limulus* compound eye [36, 37] and catfish retina [78], in that it is presumed that little signal modification occurs at the analog-to-digital conversion process. It would be interesting to see if the slow potential or the spike signals of L-neurons, or both, are encoded in the response of third-order neurons. Figs. 12B and C show typical examples of responses of third-order ocellar neurons to sinusoidally modulated light. A type of third-order neuron, OL-I neuron (type I neuron projecting into the optic lobe), had spontaneous spike activity and exhibited a modulation of the spike frequency around a mean (Fig. 12B). The pattern of the response was similar to the slow potential response of L-neurons. The other type, the D-I neuron (type I neuron descending to the thoracic ganglia), had no spontaneous spike activity and exhibited single spikes at the decremental phase of light modulation (Fig. 12C). The pattern of the response was similar to that of the spike response of L-neurons. Thus, it is concluded that both graded and spike signals of L-neurons are encoded in the spike responses of third-order neurons [48, 53]. The graded response of L-neurons appears to continuously monitor the contrast of intensity changes, whereas the spike response possibly signals an urgent event which requires rapid behavioral reactions.

Nonlinear signal processing at second synapses

Analysis of the signal transmission at synapses between second- and third-order neurons (second synapses) of the insect ocellar system was initiated by Simmons [86] who examined the operations of synapses which L-neurons make with a pair of large descending third-order ocellar neurons, DNI (an ipsilaterally descending neuron), of the locust. Both L-neurons and DNI neurons hyperpolarize when their ocellus is illuminated. L-neurons and DNI neurons produce sharply rising regenerative responses when a bright light is switched off. L-neurons make excitatory (sign-conserving) chemical synapses with the DNI neurons. Under steady daylight illumination, L-neurons continually release transmitters onto the DNI neurons. The hyperpolarizing responses of DNI neurons to an increase in illumination are due to a decrease in the rate of release of transmitter from the L-neurons.

Further detailed analyses of transfer characteristics of the second synapses of ocellar systems have been made in the cockroach. Mizunami and Tateda [52] identified nine types of interneurons in the cockroach with arborizations in the ocellar tract neuropil. When recordings were made in the ocellar tract, all types of neurons exhibited a similar response to step stimulus given in the dark, i.e., a tonic hyperpolarization during illumination and one or a few transient depolarizations at the end of illumination. These neurons can be classified into several physiological types from responses recorded in their axons or terminal regions. Some neurons exhibited spontaneous spike discharge, some neurons had no spontaneous discharge and others generated no spikes to either ocellar illuminations or extrinsic current injections into the neurons [52, Mizunami, personal observation]. Mizunami and Tateda [54] made simultaneous intracellular recordings from these neurons and L-neurons and found that these neurons receive monosynaptic inputs from L-neurons. The synapses made from L-neurons to these neurons had similar properties to those reported for the synapses made from L-neurons to DNI neurons of locusts. Excitatory (sign-conserving) synaptic transmission was tonically maintained under normal resting potentials, so that hyperpolarizing responses of L-neurons produced hyperpolarizations in third-order neurons.

Mizunami [49] further studied the transfer characteristics of synapses made from L-neurons to third-order neurons of the cockroach ocellar system using simultaneous microelectrode penetrations and the application of tetrodotoxin. The stimulus used was a sinusoidally- modulated light around a mean illuminance or an extrinsic current applied to the L-neurons. The waveform of the response of L-neurons to sinusoidally-modulated light is almost sinusoidal, which indicates that the response is linear, but the waveform of the response of third-order neurons deviates from sinusoid and exhibits a half-wave rectification, i.e., the depolarizing response to light decrement is much larger than the hyperpolarizing response to light increment (Fig. 13). Analysis of the synaptic transfer curve relating pre- and postsynaptic voltages showed that the synapses made from L-neurons to third-order neurons operate at an exponentially rising part of the overall sigmoidal transfer curve (Fig. 14). Due to the nonlinear characteristics of the synaptic transfer, the linear responses of presynaptic neurons are converted into half-wave rectified responses of postsynaptic neurons (Fig. 15A).

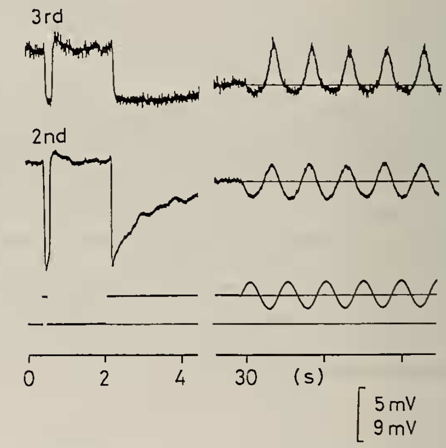

Fig. 13. Responses of a second- and a third-order ocellar neuron of the cockroach evoked either by step-stimuli given in the dark or by a sinusoidally modulated stimulus around a mean illuminance. The sinusoidal stimulus has a modulation depth of 0.7 and a modulation frequency of 2 Hz. Horizontal lines in the records are the steady (DC) potential levels maintained during steady illumination. The lowest trace indicates the stimulus light, monitored by a photodiode. Calibration: 5 mV for the third-order neuron; 9 mV for the second-order ocellar neuron. From Mizunami [49].

The properties of the second synapses of cockroach ocelli were compared to those reported for first synapses of other visual systems. In most visual systems studied thus far, both photoreceptors and second-order neurons exhibit linear responses to changes in intensity, thereby suggesting the linear nature of signal transmission at first synapses. Indeed, studies of first synapses in turtle retina [62], barnacle ocelli [28], dragonfly ocelli [87] and fly compound eyes [43] show that signal transmission occurs at the mid-region of the sigmoidal transfer curve where the transmission is linear. It is concluded, therefore, that operation ranges over the synaptic

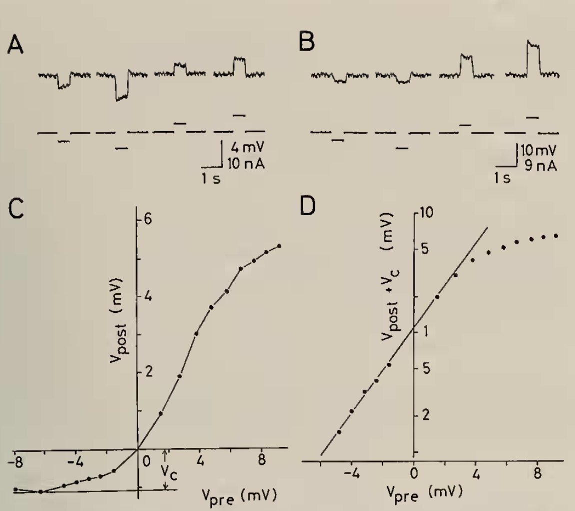

FIG. 14. Measurements of transfer characteristics of second synapses in the cockroach ocellar system. (A) Typical records of a current/voltage relationship of a second-order ocellar neuron (L-neuron) measured by impaling the neuron with two electrodes. (B) Responses of a third-order ocellar neuron evoked by current stimuli applied to an L-neuron. Averaged current-voltage relationships from six L-neurons were used to estimate presynaptic potential changes during current stimuli for the experiments in C. Actual input resistance of L-neurons deviates slightly from cell to cell (~±13%), thus, the estimated synaptic transfer curve may have slight errors. Lower traces in A and B indicate the magnitude of the stimulus current. (C) Input/output voltage relationship of the synaptic transmission. Measurements were made at the steady-state value for 0.5 sec current pulses. V_c is the synaptic potential maintained in the dark. V_{pre} and V_{post} are the potentials of the second- and third-order neuron, respectively. The potentials were measured from the dark level, thus, $V_{post}+V_c$ is the actual postsynaptic potential. (D) Semilogarithmic plot of the input/output voltage relationship of the synaptic transmission. From Mizunami [49].

transfer curve differ between first synapses and second synapses (Fig. 15B), thus resulting in fundamental differences in signal transmission, i.e., transmission is nonlinear and half-wave rectifying at second synapses whereas it is linear at first synapses.

Rectified responses have been noted in some third-order neurons of a variety of visual systems including ganglion cells of goldfish retina [91] and cat retina [16, 30], third-order neurons of locust compound eyes [32, 66, 67], locust ocelli [86], and barnacle ocelli [99]. The rectified responses seen in third-order neurons of these visual systems can be explained if their second synapses have a nonlinear rectifying nature, as do second synapses of the cockroach ocellar system.

The response of cockroach ocellar third-order neurons to brightening is much smaller than that to dimming. In barnacle ocelli, Stuart and Oertel [99] noted that the response to dimming is enhanced as signals are passed from second- to third-order neurons. Because the major function of barnacle ocelli is to detect dimming to facilitate a shadow-induced withdrawal of the animal into the shell [26], it is reasonable to

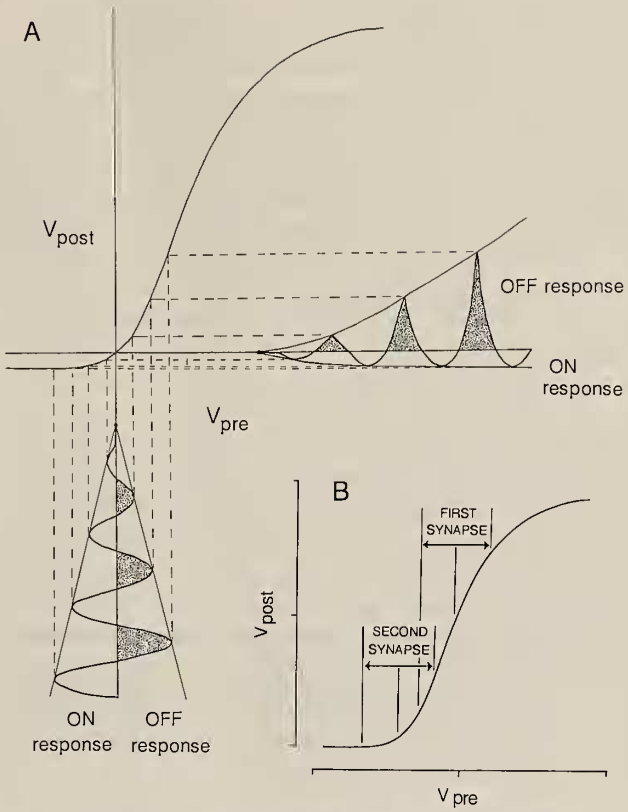

FIG. 15. Nonlinear signal transmission at second synapses. (A) Signal rectification by nonlinear synaptic transmission from second- to third-order ocellar neurons of the cockroach. Synaptic transmission occurs using an exponentially-rising part of the over-all sigmoidal transfer curve, thus, the depolarizing response to light decrement of presynaptic neurons is amplified, while the hyperpolarizing response to light increment is compressed. From Mizunami ([51]). (B) Linear and nonlinear signal transmission at graded synapses. The synapse between second- and third-order neurons (second synapse) of cockroach ocelli operates at an initially rising part of the S-shaped input/output relationship; thus, the transmission is nonlinear and rectifying. The synapse between photoreceptors and second-order neurons (first synapse) of visual systems presumably operates at a mid-region of the S-curve, where the transmission is essentially linear. From Mizunami [49].

use a large part of the dynamic range to code signal about dimming. In insect ocelli, Stange [93] studied the role of ocelli in visual steering behavior of dragonflies in flight and concluded that a decrease in illuminance of the ocelli has a strong effect on inducing steering behavior to avoid nose-diving toward the ground, whereas an increase in illumination is less effective. It appears that in these simple visual systems, the detection of dimming is more important than that of brightening, and thus dimming-specific responses are formed by removing redundant signals.

NEURAL PRINCIPLES FOR THE DETECTION AND PROCESSING OF CONTRAST SIGNALS

In this section, I will briefly summarize information

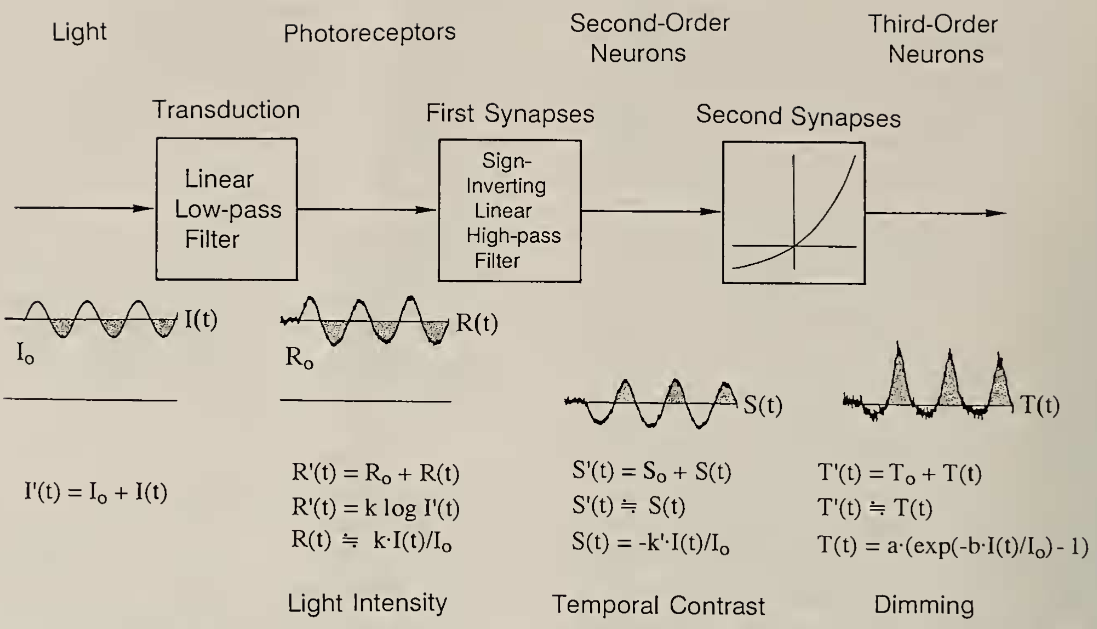

FIG. 16. Summary diagram of signal processing in the cockroach ocellar system. The light-to-voltage transduction process in photoreceptors has a linear lowpass filtering property. The photoreceptor responses encode absolute light intensity and feed into first synapses, which have a sign-inverting, linear lowpass filtering property. The response of second-order neurons, which encodes contrast of intensity changes, feeds into second synapses. The second synapse is static (frequency-independent) and has an exponential input/output relationship. The response of third-order neurons encodes dimming. From Mizunami [51].

processing in the cockroach ocellar system (Fig. 16). The light inputs which enter the ocellar photoreceptors, I'(t), consist of two components, a time-varying component, I(t), and a steady mean, I_o. The light-to-voltage transduction process in ocellar photoreceptors is linear and has a lowpass filtering property. Its output, i.e., photoreceptor response R'(t), consists of two components, a time-varying component R(t), and a steady component R_o. R(t) is related to I(t), and R_o is related to I_o. The photoreceptor response then feeds into first synapses, i.e., synapses between receptors and second-order neurons. The first synapses are linear, sign-inverting, and have a highpass filtering property. The output, i.e., the response of second-order neurons S'(t), can be divided into two components, a time-varying part S(t), and a steady mean S_o. S(t) is linearly related to the stimulus contrast $I(t)/I_o$. Because of the highpass nature of first synapses, the S_o is small. Thus, S'(t) can be written as:

$$S'(t) \fallingdotseq S(t) = -k' \, I(t)/I_o, \qquad (1)$$

where $k'(f) > 0$. To simplify the discussion, the spike response of L-neurons is not considered here. The response of second-order neurons S'(t), feeds into second synapses. The second synapses are static (frequency-independent) and have an exponential input/output relationship. The response of third-order neurons T'(t), can be written as:

$$\begin{aligned} T'(t) \fallingdotseq T(t) &= a(\exp(S'(t)/k'') - 1) \\ &= a(\exp(-b \, I(t)/I_o) - 1), \qquad (2) \end{aligned}$$

where T(t) is a time-varying component of the response of third-order neurons; $k''(f) > 0$; $a > 0$; $b(f) > 0$. Because the exponential filter enhances the response to dimming and compresses the response to brightening, the response of third-order neurons mainly codes for dimming.

This model suggests that dimming detection in the insect ocellar system is performed by a cascade of a few processing steps. Each step extracts an aspect of visual signals by removing redundant signals, so that the system can finally detect specific, biologically significant features. It can be argued that this cascade organization may reflect the pathways by which insect ocellar systems have evolved. The ocellar systems may have originated from simple photoreceptors whose functions were to detect the distribution of light intensity around the animal, and then first-order interneurons followed, enabling detection of temporal contrast signals representing the movement of self or large objects. Finally, second-order interneurons followed to specifically code for dimming, enabling the evaluation of an approach of large objects to perform an appropriate avoidance behavior. In short, the present neural circuits of the cockroach ocellar system may involve ancestral neural circuits from which the ocellar system has evolved.

DETECTION OF TEMPORAL CONTRAST AS A BASIS OF HIGHER VISUAL FUNCTIONS

Detection of temporal contrast is a basic pre-processing necessary for the extraction of biologically significant visual information such as color, motion, and shape of objects. Knowledge of the neural mechanisms for the detection of contrast signals obtained in the cockroach ocellar system, therefore, provides a basis for understanding neural mechanisms subserving advanced visual functions. Mizunami [49, 50] discussed two examples in which neural mechanisms of higher visual function can be explained by simple duplications and modifications of dimming detection circuits which represent the cockroach ocellar system. One is the neural circuit for segregating contrast signals into ON, OFF and ON-OFF channels [49], and the other is the neural circuit for detecting the direction of motion [50], both of which are major components of visual processing in advanced visual systems including insect compound eyes and vertebrate visual systems.

Formation of ON and OFF channels

Some classes of third-order neurons of vertebrates (retinal ganglion cells [76–78, 91]) and insect compound eyes [66] exhibit half-wave rectified, ON-depolarizing or OFF-depolarizing responses. These neurons form separate ON and OFF channels which specifically code for light increments and decrements, respectively. Some third-order neurons of vertebrate retinas [76, 77] and insect compound eyes [32, 66, 67] also show full-wave rectified, ON- and OFF-depolarizing responses, which form flicker-sensitive, ON-OFF channels. The reasons that signals for intensity changes are not transmitted by linear contrast detectors but by separate ON and OFF channels have been discussed by Shiller et al. [83], who pointed out that by having both ON and OFF channels, signals for both dimming and brightening can be transmitted without maintaining a high rate of spike discharges which require a high rate of metabolic activity. This allows for an economical coding of contrast. Mizunami [50] pointed out that the segregation of contrast signals into ON, OFF and ON-OFF channels can be explained if the synapses from second- to third-order neurons (second synapses) of these visual systems have a rectifying nature, as do those of cockroach ocelli (Fig. 17). Indeed, Toyoda [106] and Miller [47] proposed that the full-wave rectified response of ON-OFF amacrine cells of vertebrate retina can be explained if the cells receive half-wave rectified synaptic input from both ON and OFF bipolar cells. It is concluded that simple modification of dimming detection circuits is sufficient to explain the mechanisms to form ON and OFF channels.

Directionally-selective motion detection

Advanced visual systems such as insect compound eyes

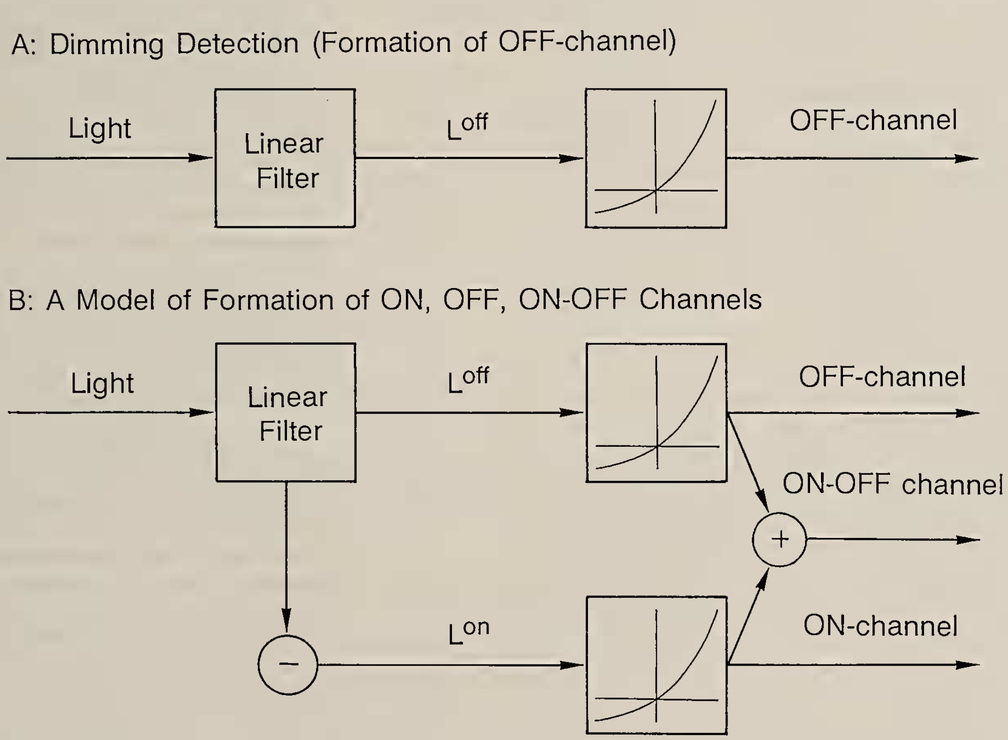

FIG. 17. Neural circuits for dimming detection and for formation of ON and OFF channels. (A) A circuitry model of dimming detection in the cockroach ocellar system, consisting of a sign-inverting bandpass linear filter followed by a synaptic rectifier with an exponential input-output relationship. The output of the linear filter, L^{off}, and that of the rectifier, OFF-channel, represents the response of second- and third-order ocellar neurons, respectively. (B) A model of a contrast detector which comprises the main structure of the movement detection circuit of Fig. 18A. L^{on} and L^{off} are on- and off-depolarizing linear responses, respectively. The outputs of the circuitry consist of three classes: on-, off-, and on-off depolarizing rectified responses. These specifically encode light increment, light decrement and flicker, respectively, and are indicated as ON, OFF and ON-OFF channels. Modified from Mizunami [50].

and vertebrate visual systems have movement detectors which code visual motion in a directionally selective manner. Behavioral and psychophysical studies show that movement detection by insects and humans can be represented by a mathematical algorithm referred to as a correlation model (Fig. 18C) [1, 27, 79]. The neural mechanism of this motion computation, however, has not been established as yet. Mizunami [50] described a model mathematically equivalent to the correlation-type movement detector (Fig. 18A). The main structure of the model is comprised of contrast detectors in Fig. 17B which consist of bandpass linear filters followed by synaptic rectifiers. Linear, one-directional, lateral interactions are assumed among the contrast detectors. Thus, the basic assumption of this model is that synapses between second- and third-order neurons of movement detection systems are nonlinear and rectifying, as are those of cockroach ocellar systems. Mizunami [50] showed that synaptic rectifiers convert linear spatial interactions into a multiplication-like (quadratic) interaction, which is the core of the correlation-type movement detector. One of the neural models, which contains both excitatory (additive) and inhibitory (subtractive) lateral interactions among contrast detectors (Fig. 18B), well approximates the correlation model (Fig. 18C, D) in both time-averaged and dynamic (instantaneous) responses. Some of the basic features of the model agree with those of actual movement detector neurons of insects [50].

Evolutionary perspective

I have shown that: (1) step-by-step modifications of simple photoreceptors are sufficient to explain the evolution of dimming-detection circuits of cockroach ocelli; (2) simple modifications and duplications of dimming-detection circuits are sufficient to explain contrast coding circuits with separate ON and OFF channels; and (3) simple modifications and duplications of contrast coding circuits with separate ON and OFF channels are sufficient to explain neural circuits for motion detection. These findings imply that complex neural circuits subserving advanced visual functions have evolved through step-by-step modifications of simper neural circuits subserving simpler visual functions, and that the present complex neural circuits contain, at least in part, simple neural circuits from which the present neural circuits have evolved. I conclude that careful comparison of neural circuits of

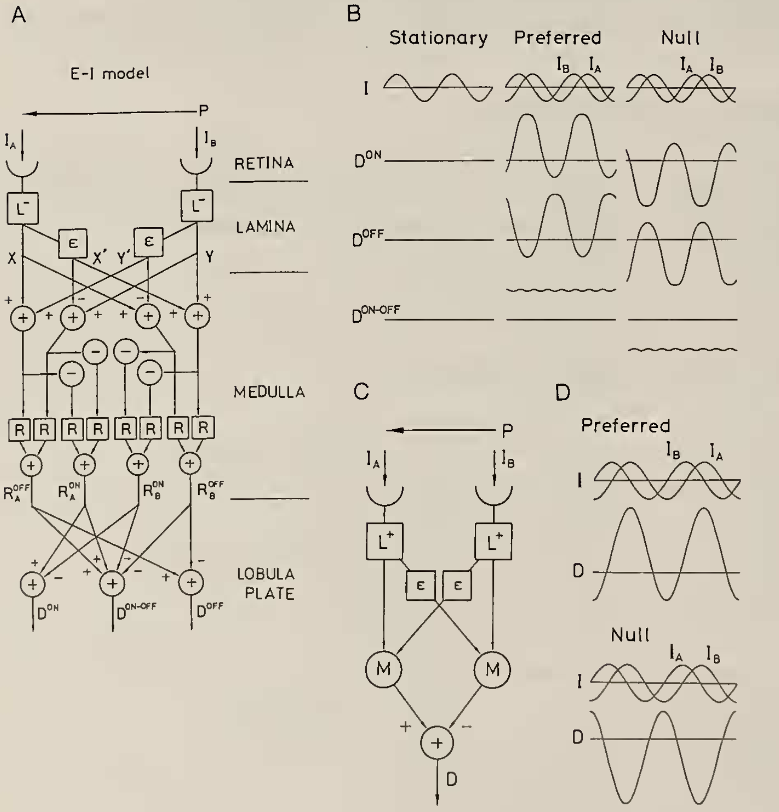

Fig. 18. Computational and neural models for motion detection. (A) A model of neural circuits for directional-selective motion detection. Possible location of each process in a fly's compound eye is illustrated (*right*). The model (E-I model) consists of one-directional linear interactions among contrast-detection circuits of Fig. 17B. The model involves both excitatory and inhibitory lateral interactions. I_A and I_B are inputs to left and right detectors. L- is a sign-inverting bandpass linear filter, the output of which approximates the response of lamina monopolar cells. ε is a sign-conserving lowpass linear filter. R is a synaptic rectifier with an exponential input/output relationship. Lateral interaction and rectification may take place in the medulla neuropil. On- and off-depolarizing linear responses feed into rectifiers, producing on- and off-depolarizing rectified responses, R^{on} and R^{off}. R^{on} and R^{off} are assumed to represent responses of ON- and OFF-EMDs (elementary movement detectors). The final outputs of the models consist of three classes, D^{on}, D^{off} and $D^{\text{on-off}}$. The model outputs may represent responses of motion-sensitive neurons of the lobula plate. P is the preferred direction of motion. (B) Responses of the E-I model to a stationary flickering light and to a sinusoidal grating moving in the preferred and null directions. The ON-OFF motion detector ($D^{\text{on-off}}$ in A) exhibits a steady response to motion, whereas responses of ON and OFF motion detectors (D^{on} and D^{off}) oscillate, depending on the spatial phase of the stimulus pattern. The stimulus parameters are: 1) for response to motion in the preferred direction, the phase lag due to the spatial separation of left and right input channels, ϕ_s, is $\pi/2$ and the phase lag due to the delay in lateral interaction, ϕ_t, is $\pi/2$; 2) for response to motion in the null direction, $\phi_s=\pi/2$ and $\phi_t=-\pi/2$; and 3) for response to a stationary flickering light, $\phi_s=0$ and $\phi_t=\pi/2$. (C) The correlation model proposed by Hassenstein and Reichardt [27]. L^+ and ε are sign-conserving, lowpass linear filters. M is a multiplier. D is the final output. (D) Responses of the correlation model to a sinusoidal grating moving in the preferred and null directions. The stimulus parameters are the same as for (B). From Mizunami [50].

different animals is an effective approach to understanding possible evolutionary pathways by which complicated neural circuits of animal brains have formed.

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